# The influence of tree species and edge effects on pheromone trap catches of oak processionary moth *Thaumetopoea processionea* (L.) in the U.K.

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**Abstract**
1 Many factors influence the efficiency of insect pheromone trapping systems. In particular, captures of male oak processionary moth (OPM) *Thaumetopoea processionea* in pheromone traps can be highly variable, hence, two trials were conducted to determine whether the tree species in which traps are positioned or edge effects are influential factors in OPM pheromone trapping.

2 In a 'host plant trial', pheromone traps that were positioned in the canopy of pedunculate oak (*Quercus robur*) trees captured significantly more male OPM than traps positioned in any of the other six tree species (including other species of oak) used in the trial over two successive years.

3 In an 'edge effects trial', pheromone traps positioned on the edges of oak woodland blocks captured more moths than traps positioned within the oak woodland itself.

4 Although wind direction influenced the numbers of moths that were captured in pheromone traps on woodland edges, with more moths captured in traps positioned on sheltered north-facing edges, the differences in trap catches between north, south, east and west edges were not significant.

5 The results from the present study indicate that a greater emphasis should be taken to deploy pheromone traps for oak processionary moth in the canopies of pedunculate oak trees with an open, sunnier disposition rather than within the interior of the forest or woodland, thereby maximizing their efficiency.

**Keywords** Lepidoptera, monitoring, pheromones, *Quercus* spp., trapping.

## Introduction

The oak processionary moth (OPM) *Thaumetopoea processionea* (L.) is a widely distributed Lepidopteran pest of oak *Quercus* spp. in western, central and southern Europe (EFSA, 2009). The larvae can be serious defoliators of oak trees and, in combination with other defoliating insects and pathogens, they are likely to be a significant contributing factor to oak decline in general, particularly in drought years (Thomas *et al.*, 2002; EFSA, 2009). In addition, the late-instar larvae of OPM are a public health concern because the larvae have urticating hairs that can cause a wide range of health issues in humans and animals, including dermatitis, pruritus, respiratory and ophthalmic issues and, in rare cases, anaphylactic reactions (Public Health England, 2015).

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The moth was accidentally introduced into the U.K. via the importation of infested oak trees, and since the discovery of larvae in 2006 in west London it has slowly spread over a wider area despite eradication and subsequent containment efforts (Townsend, 2008 & 2009; Cowley *et al.*, 2015). Monitoring the spread of OPM has been an integral part of the attempts to manage and control this invasive insect pest, and hence the development and use of an effective pheromone trapping system has been essential (Straw *et al.*, 2013; Williams *et al.*, 2013). For rapid action, it is vitally important to ensure that an efficient monitoring system is utilized to inform landowners as early as possible that OPM has reached previously uninfested trees in woodlands, parks and other amenity areas. However, many factors influence the effectiveness of trapping systems for insect pests, particularly pheromone trapping for Lepidoptera pests (Cardé & Elkinton, 1984; Muirhead-Thompson, 1991). Although pheromone trapping is an effective method of detecting

the presence of OPM in a given area, the positioning of the trap in the canopy is critical with respect to ensuring its efficiency. Previous studies have shown that traps need to be positioned high in the tree canopy, ideally above 10 m, to be most successful at capturing male OPM (Breuer *et al.*, 2003; Williams *et al.*, 2013). Other factors are likely to be just as influential and the potential role of the host plant in which the pheromone trap is positioned may be one such factor that has not been considered previously.

OPM is generally regarded as a monophagous insect pest feeding solely on *Quercus* species across Europe (Fransen, 2013; Sobczyk, 2014; Battisti *et al.*, 2015). Adults emerge in the summer months (July to mid-September), with female moths ovipositing eggs on the terminal branches of oak trees high in the canopy (Battisti *et al.*, 2015). Eggs hatch the following spring (April to early May) and this is generally well synchronized with oak bud flushing, although neonate larvae are able to withstand up to 3 weeks of starvation, reflecting the adaptability of the species to the variable bud-burst phenology within and between oak trees (Meurisse *et al.*, 2012; Battisti *et al.*, 2015). Although there are reports of OPM larvae feeding on other tree species, there is no published information available confirming that its development to the adult stage can be completed on any of these other tree species, although, for beech (*Fagus* spp.), it has been cited as a possibility (Stigter *et al.*, 1997). Across Europe OPM has been found primarily associated with *Quercus robur* (L.), *Quercus petraea* (Matt.) Liebl., *Quercus cerris* (L.) and *Quercus pyrenaica* (Willd.), although it has been observed on many other oak species, including some North American species such as *Quercus rubra* (L.) in botanical gardens, arboretums and amenity areas (Pascual, 1988; Stigter *et al.*, 1997; Fransen, 2013; Jäckel, 2013; Sobczyk, 2014). Because woodlands and amenity areas are commonly planted with a wide range of tree species, it is particularly important to establish whether the positioning of pheromone traps for OPM needs to be in oak trees or whether it can be just as effective to place pheromone traps in other tree species. There are now many examples demonstrating that plant volatiles (semiochemicals) can synergistically enhance the response or modify the behaviour of a male insect to the female sex pheromone (Landolt & Phillips, 1997; Reddy & Guerrero, 2004; Bruce & Pickett, 2011; Xu & Turlings, 2018). Although most studies describe the synergistic improvements that plant volatiles have on male insects responding to the female sex pheromones, there are also examples where plant volatiles can inhibit or repel insects (Reddy & Guerrero, 2004). In pine processionary moth *Thaumetopoea pityocampa* (Denis & Schiffermüller), the behaviour of male moths was detrimentally affected by the presence of non-host plants, resulting in fewer male moths being captured in pheromone traps (Jactel *et al.*, 2011), and studies on other insect herbivores have demonstrated that vegetation diversity can affect the population ecology of the insect (Tahvanainen & Root, 1972). Hence, plant volatiles from both host plants (*Quercus* spp.) and non-host plants may be influential factors in male OPM orientating to the female moth pheromone and so it is of some relevance to establish whether male OPM catches in pheromone traps are influenced favourably or detrimentally, depending on the tree species that the pheromone traps are positioned in.

OPM has been described as a thermophilic species (Battisti *et al.*, 2015) and its affinity for sunlit, open areas influences not only where nests are likely to be positioned in the canopy of individual trees, but also where OPM nests are likely to occur in forest and woodland blocks (Sobczyk, 2014). There is general consensus that OPM prefers forest and woodland edges, open forests, and the sunlit, open crowns of either individual or groups of trees, particularly in urban environments (Stigter *et al.*, 1997; Offenberg, 2000; Sobczyk, 2014; Battisti *et al.*, 2015). Even the density of trees within forest or woodland blocks is likely to have a significant influence on the distribution and frequency of OPM nests, which in turn would affect the numbers of moths captured in pheromone traps. Observations of pine processionary moth within stands of pine have found that more nests are generally discovered not only in more open pine stands, but also more likely to be located towards the edges of forest stands, particularly south-western edges (Samalens & Rossi, 2011; Dulaurent *et al.*, 2012; Barbaro *et al.*, 2013; Régolini *et al.*, 2014). Similarly, for gypsy moth *Lymantria dispar* (L.), another serious defoliating Lepidoptera pest associated with oak trees, studies have shown that more male moths are captured in pheromone traps positioned on the forest edges compared with the forest interior, and also that greater rates of defoliation are observed on forest edges rather than within the forest interior (Dulamsuren *et al.*, 2010; Thompson *et al.*, 2016). This suggests that a similar trend may also occur for OPM and that, within oak forests and woodlands, more nests are likely to be found either towards the edges of blocks of trees, in more open woodland blocks, or on solitary trees, and hence more male moths may be captured in pheromone traps positioned on the edges rather than within the interior of the forest or woodland blocks.

To investigate some of these other potential factors affecting the pheromone trapping efficiency of OPM, two trials were conducted: a 'host plant trial' and an 'edge effects trial'. The host plant trial aimed to establish whether pheromone traps for OPM needed to be positioned within oak trees to capture male OPM effectively or whether traps could be just as effective when positioned in the canopy of other tree species. Furthermore, if pheromone traps are more effective when positioned in oak trees, does the species of oak itself have any influence on the numbers of moths that a trap catches. The edge effects trial aimed to investigate whether pheromone traps for OPM were more effective when positioned on the edges of oak woodlands rather than within the woodland block itself and, in addition, when traps are positioned on woodland edges, whether aspect influences the trap capture rates. The aim of the two trials was essentially to investigate the potential factors that influence male OPM capture rates in pheromone traps and to determine whether it was possible to improve the current pheromone trapping methodology for OPM. By optimizing the trapping method further, this ensures that the detection system for the moth is as effective as possible, which is vitally important since the moth continues to spread into more rural areas south and west of the current outbreak area in west London.

## Materials and methods

### Study site

The experimental trials were carried out in Richmond Park, west London (National Grid Reference: TQ 201730), which is the

largest of the Royal Parks in London, covering an area of almost 1000 ha. The park has over 100 000 trees of which approximately 40 000 are oak trees, mainly *Q. robur* (L.), although some other oak species are planted in various locations as ornamentals. The park was selected for the experimental trial because it was located within the main OPM outbreak area, and a large number of oak trees in the park and in the surrounding area have been infested with OPM from at least 2009 onwards.

### Host plant trial

In 2014 and 2015, the host plant trial aimed to investigate whether positioning pheromone traps for OPM in different tree species had any influence on the capture rates of male OPM within the traps. All trees selected for the trial were at least 15 m in height, had a diameter at breast height (dbh, 1.3 m above the ground) ranging from 46 to 170 cm, and were relatively accessible from a path, track or road. In total, 84 trees were selected, with 12 pheromone traps positioned in the canopies of seven tree species, which included pedunculate oak *Q. robur* (L.), Turkey oak *Q. cerris* (L.), pin oak *Q. palustris* (Münchh.), red oak *Q. rubra* (L.), Scots pine *Pinus sylvestris* (L.), horse chestnut *Aesculus hippocastanum* (L.) and sycamore *Acer pseudoplatanus* (L.). Each tree was located at least 50 m away from any of the other selected trees to minimize the effects of trap-poaching from one pheromone trap to another; hence, a single trap was placed in any given tree. The OPM pheromone lures were obtained from Pherobank (The Netherlands) and the pheromone traps used were the standard green funnel traps supplied by Oecos (Kimpton, U.K.). All traps were positioned in the tree canopy between approximately 10 and 16 m from the ground because previous studies have demonstrated that, at this height, there is a greater efficiency at catching male OPM in pheromone traps (Breuer *et al.*, 2003; Williams *et al.*, 2013). The positioning of traps at this height in the canopy was achieved using a set of carbon-fibre telescopic poles (Telsys Ltd, U.K.), which enabled a weight attached to a polyethylene throw-line to be dropped over a suitable branch in the tree canopy. The weight was subsequently removed and a pheromone trap was attached to the line, which could then be pulled up into the correct position just below the branch in the canopy and the other end of the polyethylene throw-line was subsequently tied off on a suitable lower branch at approximately 3 m. The line could then be reached and untied from a step ladder, and the trap raised and lowered as required.

Trapping was conducted over two field seasons in 2014 and 2015, with pheromone traps positioned in the same trees (but not necessarily in the same branches) in each year. All traps were established and primed with the pheromone lure in mid-July in each year and approximately 250 mL of saline solution was added to the bucket section of the funnel trap. The traps were subsequently checked every 2 weeks until mid-September for moth captures, which covered the main OPM flight period in the U.K. (Williams *et al.*, 2013). On each collection date, moths were removed from the funnel traps and the saline solution was replaced. In addition, on the second collection date (4 weeks into the trial), the pheromone lure in each trap was replaced with a fresh lure. Moths caught in the funnel traps were placed in numbered plastic containers and taken back to the laboratory to confirm their identification.

### Edge effects trial

In 2016, the edge effects trial evaluated the efficiency of the pheromone traps when they were placed in pedunculate oak *Q. robur* (L.) trees positioned either on the edges of woodland blocks or within the woodland block itself. All 96 *Q. robur* trees selected for the trial were again at least 15 m in height, with the diameter at breast height of the trees ranging from 35 to 193 cm.

The experimental set-up and methodology was identical to the host plant trial in terms of positioning of pheromone traps in the tree canopies (i.e. standard green funnel traps, pheromone lures from Pherobank, and traps positioned in the canopy between approximately 10 and 16 m from the ground using telescopic poles). The woodland blocks used in this trial were almost entirely composed of *Q. robur* with relatively low numbers (< 5%) of other broadleaved tree species occasionally being present. In total, 96 *Q. robur* trees were selected for the edge effects trial, with 48 pheromone traps positioned in the canopy of trees within woodland blocks and a further 48 traps positioned in the canopy of trees on the edges of woodland blocks. Furthermore, the 48 pheromone traps on the edges of woodland blocks were sub-divided further so that 12 pheromone traps were positioned on predominantly north, south, east or west facing edges. This partly was to ensure that no preference was given to any particular aspect when comparing edge and within block pheromone trap catches, as well as to investigate whether there were any actual differences in positioning traps on woodland edges facing the four cardinal directions. Pheromone traps located in trees within a woodland block were positioned in the canopy of oak trees that were at least 30 m from the edge of the woodland and had at least one other tree in front of them before reaching the open edge of the woodland itself.

Similar to the host plant trial, all pheromone traps were established and primed with the pheromone lure in mid-July 2016 and 250 mL of saline solution was added to the bucket section of the funnel trap. Traps were subsequently checked every 2 weeks until mid-September for moth captures and, on each collection date, moths were removed from traps and the saline solution was replaced. In addition, on the second collection date (4 weeks into the trial), the pheromone lure in each trap was replaced with a fresh lure.

### Meteorological data

Meteorological information, particularly wind direction data, was obtained from the Met Office MIDAS data set for two weather recording stations close to Richmond Park (Met Office, 2006). The Kew Gardens MIDAS recording station (Grid ref. TQ 185772) is approximately 3 km north of Richmond Park and the Heathrow MIDAS recording station (Grid ref. TQ 076767) is approximately 11.5 km north-west of Richmond Park. The meteorological data obtained from each MIDAS recording station comprised hourly wind direction and speed information for the month of August 2016, which covered the main flight period of OPM (Williams *et al.*, 2013). The data

set obtained summarized the average prevailing wind direction for each hour and essentially comprised a compass bearing in degrees representing the direction from which the wind was coming from. Hence, for August, there were 744 hourly records of prevailing wind direction for the two weather recording stations. The data were summarized further by assigning each of the individual hourly compass bearings to one of eight compass directions (N, NE, E, SE, S, SW, W, NW) and, subsequently, the percentage of the bearings that came from a particular direction was calculated for each weather recording location. This information was then used to determine whether it influenced trap catches of male OPM in pheromone traps positioned on either the north, east, south or west edges of woodland blocks.

### Statistical analysis

The data obtained from the host plant trial were analyzed using a generalized linear mixed model (GLMM) with Poisson error distribution and logarithmic link function. Tree species and year were entered as fixed effects in the model, and trap number (a unique trap identification number for each individual trap, from 1 to 84) was defined as a random effect in the model. When a significant result occurred from the GLMM analysis, Fisher's unprotected least significance test was used to identify where the significant differences ($P < 0.05$) occurred between the seven tree species.

Data obtained from the edge effects trial, which were not normally distributed, were analyzed using a Mann–Whitney test to compare total trap catches between pheromone traps positioned either within a woodland block or on the edges of the block. A Kruskal–Wallis test was used to compare traps positioned on the four different cardinal directions of the edges of woodland blocks.

Capturing single OPM in pheromone traps is relatively uninformative because male moths are relatively strong fliers and are reputedly capable of flying tens of kilometres (Battisti *et al.*, 2015); hence, it is of more interest from a management perspective to consider traps that capture a reasonable number of moths. It is difficult to set a 'threshold' trap catch that would alert landowners of the presence of OPM in the immediate vicinity of the trap; however, experience from the Netherlands suggests that a pheromone trap catch of five or more moths is sufficient to instigate survey and controls in close proximity (within 500 m) to the pheromone trap (H. Kuppen, personal communication). Hence, we used Fisher's exact test to determine whether there were any significant differences in the ability of OPM pheromone traps positioned either within or on the edges of woodland blocks to capture either five or more moths, or 10 or more moths.

All statistical analyses were performed using GENSTAT, version 16 (Payne *et al.*, 2013).

## Results

### Host plant trial

In total, 579 male OPM were captured in the 84 pheromone traps across both years of the trial, with slightly more male OPM captured in 2014 (334 moths) than in 2015 (245 moths). However, the distribution of male moths captured in the pheromone traps positioned in each tree species remained proportionally the same each year, with considerably higher numbers of male OPM moths being captured in traps positioned in *Q. robur* in both years (Fig. 1). Out of the 579 male moths captured, 272 (47%) were captured in traps positioned in *Q. robur*, which was almost three times as many moths captured than in traps in the next apparently favourable tree species *Q. rubra*, which captured 95 moths (16.4%). Traps positioned in *A. hippocastanum* and *A. pseudoplatanus* captured slightly fewer moths than those positioned in *Q. rubra*, with total trap catches of 70 moths (12.1%) and 66 moths (11.4%), respectively. Pheromone traps positioned in the other tree species did not appear to perform particularly well at all, with traps in *Q. cerris*, *Q. palustris* and *P. sylvestris* only catching 36 moths (6.2%), 26 moths (4.5%) and 14 moths (2.4%), respectively, across the 2 years (Fig. 1). The GLMM analysis revealed that there were significant differences in the total number of male OPM moths captured in the pheromone traps between each tree species (Wald's $\chi^2 = 48.1$, d.f. = 6, $P < 0.001$). Further analysis of the data revealed that pheromone traps positioned in *Q. robur* captured significantly higher numbers of moths than traps positioned in any of the other tree species (Fisher's unprotected least significant difference test, $P < 0.05$) (Fig. 1).

Only 33 out of the total 168 pheromone traps (19.6%) operating across the 2 years of the trial captured five or more moths. Pheromone traps positioned in *Q. robur* were more likely to capture five or more moths, with 14 out of 24 traps (58.3%) doing so compared with only nine traps (37.5%) in *Q. rubra*, six traps (25%) in *A. hippocastanum*, three traps (12.5%) in *A. pseudoplatanus* and one trap (4.2%) in *Q. cerris*. Traps positioned in either *Q. palustris* or *P. sylvestris* failed to capture five or more moths in any trap in either of the 2 years of trapping. Unfortunately, because most traps (135 traps; 80.4%) in this trial captured less than five moths, the data set did not lend itself to further statistical analysis. However, the observation that more than half of the traps positioned in *Q. robur* captured five or more
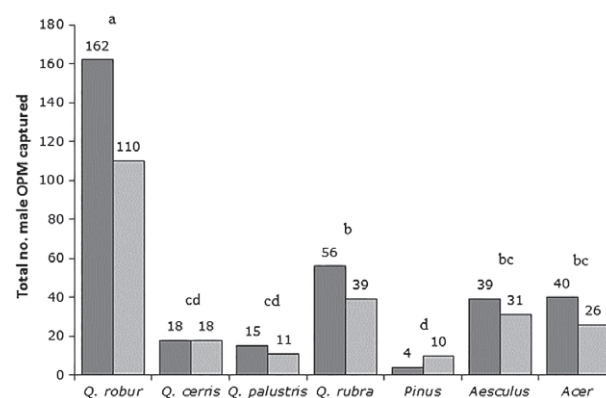


**Figure 1** The total number of adult male *Thaumetopoea processionea* captured in pheromone traps positioned in the canopy of the seven tree species used in the host plant trial in 2014 (dark grey) and 2015 (light grey). Tree species with different lowercase letters indicate significant differences in the numbers of total male oak processionary moth (OPM) captured (Fisher's unprotected least significant difference test, $P < 0.05$).

moths demonstrated at the very least that the higher numbers of male moths in *Q. robur* traps was not simply a result of a couple of traps catching an inordinately high number of moths.

### Edge effects trial

In total, 787 moths were captured in the 96 pheromone traps in the 2016 edge effects trial, with 573 moths (72.8%) captured in traps positioned on the edges of woodland blocks compared with only 214 moths (27.2%) captured in traps positioned within the woodlands. This difference was highly significant (Mann–Whitney, $U = 605.5$, $P < 0.001$) (Table 1) and clearly demonstrated that pheromone traps positioned on the edges of woodlands were more effective at capturing male OPM than traps located within the woodland itself. In addition, 34 of the 48 pheromone traps (70.8%) positioned on woodland edges captured five or more male moths compared with only 13 out of 48 traps (27.1%) positioned within the woodland block itself and this difference was highly significant (Fisher's exact test, $P < 0.0001$) (Table 1). Furthermore, 22 pheromone traps (45.8%) positioned on the edges of woodlands captured 10 or more male moths compared with only seven traps (14.6%) located within the woodland and, again, this difference was significant (Fisher's exact test, $P < 0.01$) (Table 1).

Of the 573 moths that were captured in edge traps, a majority of 224 moths (39.1%) were captured in pheromone traps positioned on north facing edges (Table 2). Pheromone traps positioned on east facing edges captured 147 moths (25.6%), whereas traps positioned on either the south (103 moths; 18.0%) or the west (99 moths; 17.3%) facing edges tended to capture fewer moths.

**Table 2** Total numbers and range in trap catches of adult male *Thaumetopoea processionea* caught in pheromone traps positioned on woodland edges, along with the number of traps that caught at least five moths ($n = 12$ trap on each aspect)

| Trap position | Total number of moths captured | Range in trap catch (minimum – maximum) | Number of traps capturing ≥ 5 moths |
|---|---|---|---|
| North | 224 (39.1%) | 3–47 | 10 (83.3%) |
| East | 147 (25.6%) | 0–46 | 7 (58.3%) |
| South | 103 (18.0%) | 1–38 | 8 (66.7%) |
| West | 99 (17.3%) | 0–18 | 9 (75.0%) |

Despite pheromone traps on the north facing edges tending to capture more moths than traps facing other aspects, there was no significant difference in the numbers of male OPM that were captured in traps positioned on the four cardinal direction facing edges of woodland blocks (Kruskal–Wallis adjusted for ties, $H = 6.21$, $P = 0.102$) (Table 2).

### Meteorological data

The wind direction data obtained for August 2016 for the two meteorological MIDAS recording stations at Kew and Heathrow revealed that the wind direction was predominantly (> 50% of the month) coming from either a south-westerly (Kew: 31.0%; Heathrow: 24.2%) or westerly (Kew: 24.3%; Heathrow: 28.1%) direction during the main flight period of OPM in this particular year (Fig. 2). This clearly had an influence on

**Table 1** Total numbers of adult male *Thaumetopoea processionea* captured in pheromone traps, as well as the number of traps that caught at least one, five or ten moths, in the edge effects trial conducted in 2016 ($n = 48$ traps positioned either on the edge or within woodland blocks)

| Trap position | Total number of moths captured[1] | Number of traps that captured | | |
|---|---|---|---|---|
| | | ≥ 1 moth | ≥ 5 moths[2] | ≥ 10 moths[2] |
| Edge | 573 a | 46 (95.8%) | 34 (70.8%) a | 22 (45.8%) a |
| Within | 214 b | 41 (85.4%) | 13 (27.1%) b | 7 (14.6%) b |

Values in columns with different lowercase letters are significantly different, either by the Mann–Whitney test[1] ($P < 0.001$) or Fishers exact test[2] ($P < 0.01$).
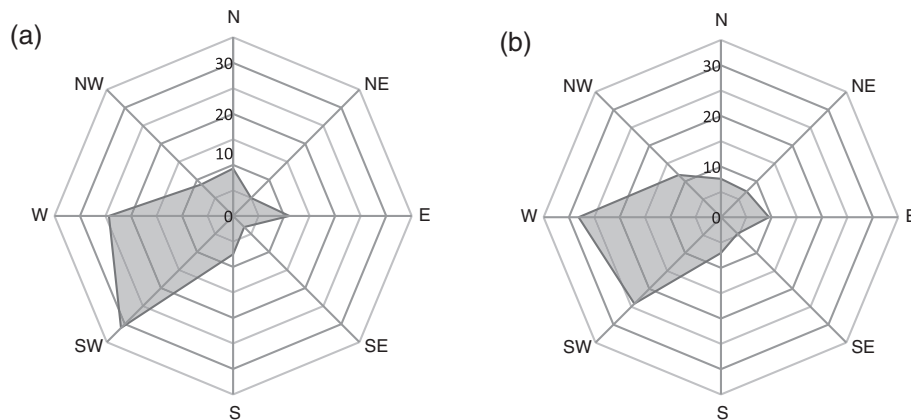


**Figure 2** Meteorological MIDAS recording station data illustrating the predominant prevailing wind direction in August 2016 for (a) Kew and (b) Heathrow.

pheromone trap catches because traps positioned on the edges of woodland blocks that were sheltered, and hence protected from the prevailing wind (i.e. more northern and eastern facing sides), tended to capture the majority (64.7%) of the moths (Table 2).

## Discussion

The results from the present field trials demonstrate that the positioning of OPM pheromone traps in different tree species and their location within the woodland block itself are clearly influential factors affecting trap captures. The host plant trial indicated that the most effective tree species to position pheromone traps for OPM in was pedunculate oak (*Q. robur*), whereas the edge effects trial clearly demonstrated that pheromone traps for OPM were more effective, and also captured more moths, when positioned in the canopies of trees on the edges of woodlands rather than being located within the interior of the woodland.

The observation that significantly more male moths were captured in pheromone traps when they were positioned in *Q. robur* suggested that the moths were orientating specifically to traps in this tree species for a reason, and hence that they may have been influenced by the volatile components of the foliage. Numerous studies have demonstrated that plant volatile organic compounds (VOCs), particularly green leaf volatiles, can be highly influential in attracting and repelling insects (Reddy & Guerrero, 2004; Bruce & Pickett, 2011; Xu & Turlings, 2018). Since OPM is a monophagous insect feeding only on *Quercus* spp., adult moths need to be able to orientate to specific host plants to maximize their reproductive success. Olfactory cues are likely to play an important role in this process, with adult moths potentially being able to detect specific or blends of VOCs that their host plants emit, hence enabling females to lay eggs on suitable hosts and ensuring that males can orientate to females on suitable host plants. There is now increasing evidence demonstrating that host plant volatiles, particularly isoprenoids, can enhance the response of some insects to sex pheromones, and this synergism between host plant volatiles and pheromones is considered to contribute to a greater success in finding a mate (Landolt & Phillips, 1997; Reddy & Guerrero, 2004; Bruce & Pickett, 2011; Xu & Turlings, 2018). Furthermore, in Lepidoptera, there is growing evidence suggesting that host plant volatiles can play a role in females orientating to host plants for oviposition (Leather, 1987; Renwick & Chew, 1994; Honda, 1995) and that males can have enhanced synergistic responses to female sex pheromones when combined with host plant volatiles (Dickens *et al.*, 1993; Light *et al.*, 1993; Ochieng *et al.*, 2002; Yang *et al.*, 2004; Varela *et al.*, 2011; Li *et al.*, 2012).

VOCs were not assessed in the present study. However, many other studies have investigated the VOC profile of numerous tree species, including *Quercus* spp., and these studies provide a useful insight into some of the differences between the individual species of oak used in the present study (Pearse *et al.*, 2013). A study by Loreto (2002) classified *Quercus* species based on their isoprenoid (isoprene and monoterpene) emissions, with the European species *Q. robur* and the North American species *Q. rubra* and *Q. palustris* all being classified as isoprene emitters, and with the European *Q. cerris* being classified as a non-isoprenoid emitter. Since *Q. cerris* is one of only a few *Quercus* species that have been identified as being a non-isoprenoid emitting tree species (Steinbrecher *et al.*, 1997; Csiky & Seufert, 1999; Loreto, 2002), this may be a contributory factor explaining why, when pheromone traps are positioned in this tree species, relatively few male OPM are actually captured. We hypothesize that, because *Q. cerris* does not emit isoprenoids, there is no synergistic enhancement of male attraction to the female sex pheromone (nor does it repel male OPM); hence, the pheromone is simply acting as a single component when traps are placed in this particular tree species. In contrast, because significantly higher numbers of male OPM were captured in traps positioned in *Q. robur*, it is feasible to hypothesize that these trees may release a specific volatile component or a blend of volatile components enhancing the response of the male to the pheromone lure, thereby leading to a synergistic effect, which perhaps explains the greater trap catches of moths in this particular species of oak.

The indifferent response of male moths to traps positioned in North American species of oak is perhaps not unsurprising because both *Q. palustris* and *Q. rubra* are unlikely to be widely distributed within the moths existing geographical region (they are likely to only occur in amenity areas and arboretums) and hence OPM will only encounter these two species of oak relatively infrequently. Despite both of these oak species being isoprenoid emitters, they are likely to have VOC composition profiles that the adult moths are either unfamiliar with or may potentially even be repelled by. Although reasonable numbers of male OPM were captured in traps positioned in *Q. rubra* in the host plant trial, and despite there being recorded incidences of *Q. rubra* being utilized by OPM (Jäckel, 2013; Sobczyk, 2014), it does not appear to be frequently or preferentially selected by OPM (Fransen, 2013). This also tends to be the case in Richmond Park where it is only occasionally utilized because OPM nests are only infrequently observed (G. Jonusas, personal observations). By contrast, *Q. palustris* does not appear to be utilized by OPM (Judeich & Nitsche, 1895 cited in Sobczyk, 2014) and this tends to be confirmed by there being no observations of any OPM nests being seen in this oak species within Richmond Park, despite the high population density of OPM within the immediate area (G. Jonusas, personal observations). This could potentially be a result of *Q. palustris* releasing a specific, or blend of VOCs that repels adult OPM. It is known to release high quantities of isoprene (Karlik & Winer, 2001) as a component of its VOCs and this may repel adult OPM moths, although so may other components in the VOC blend. Isoprene, along with other isoprenoid, phenolic and alkaloid compounds, has been shown to deter insect feeding in a wide range of plant species (Keeling & Bohlmann, 2006; Laothawornkitkul *et al.*, 2008; Eyles *et al.*, 2010; Holopainen & Gershenzon, 2010; Boeckler *et al.*, 2011). In studies on pine processionary moth (PPM), Jactel *et al.* (2011) demonstrated that non-host volatiles from birch can inhibit the response of male PPM to pheromone traps, which at least indicates that volatiles from the foliage of some tree species can also act antagonistically, deterring the attraction of moths to pheromone traps.

Studies by Jactel *et al.* (2006) reported that, for PPM, more moths were captured when pheromone traps were positioned in the upper crown of the tree and they proposed that this may be due to a synergistic effect between the pine tree VOCs and the

pheromone. In a similar manner, this may explain why OPM pheromone traps are more effective when positioned high in the tree canopy rather than below the tree canopy (Williams *et al.*, 2013). Furthermore, the orientation of female PPM to host plants is also considered to be influenced by the composition of the volatile components emitted from the needles (Jactel *et al.*, 2015). This perhaps explains why, although relatively few male OPM were captured in pheromone traps positioned in *Q. cerris*, this species of oak is selected by female OPM for oviposition of eggs, since nests are commonly found in this particular tree species, perhaps indicating females are orientating to specific olfactory cues that are not apparent to the males.

Further studies are clearly needed to investigate the role that plant volatile organic components have on the orientation behaviour of adult OPM to their host plant. This in turn could theoretically lead to improvements in pheromone lures to attract males to traps, and also offer an explanation as to not only why females orientate to specific oak species, but also why some individual trees appear to be preferentially selected over others.

The results from the edge effects trial clearly demonstrated that positioning pheromone traps on the edges of woodlands was far more effective at capturing male OPM than positioning traps within the woodland itself. Similar findings have been reported with other Lepidopteran pests of trees in that greater numbers are captured when traps are positioned on the boundaries of blocks of trees (Allen *et al.*, 1986; Athanassiou *et al.*, 2004; Thompson *et al.*, 2016). Perhaps of greater relevance is that the adults of other processionary moth species also appear to orientate to host trees in a similar manner, with more moths generally captured in traps located on forest edges or in more open habitats. Einhorn *et al.* (1983) found that pheromone traps positioned on the edges of pine stands captured significantly more male pine processionary moth than traps situated within the interior of the pine stand and Houri and Doughan (2006) found that a trap located closer to the forest edge captured more eastern pine processionary *Thaumetopoea wilkinsoni* (Tams) moths than a trap located within the forest. Athanassiou *et al.* (2007) and Bonsignore and Manti (2013) both observed that trap captures of PPM did not differ between edge and within pine stand locations; however, in both studies, more moths were captured in open, low density stands, suggesting a preference for lighter, sunnier situations. Other studies have generally confirmed this inclination and have revealed that PPM nests are more abundant on trees located at the forest edges, indicating a clear preference for female moths to orientate preferentially to edge trees (Samalens & Rossi, 2010; Dulaurent *et al.*, 2012; Regolini *et al.*, 2014). Similarly, gypsy moth egg masses are generally found in greater abundance on the edges of forests, which subsequently leads to greater defoliation being observed on trees on forest edges (Bellinger *et al.*, 1989; Hauck *et al.*, 2008; Dulamsuren *et al.*, 2010).

Trees on the edges of forests and woodlands inevitably experience more sunlight, a factor that processionary moths prefer, although they are also likely to experience greater variability in other abiotic factors such as temperature and air movement, with the latter influencing the dispersal of pheromones. The OPM pheromone plume emanating from the trap is unlikely to be effective over a long range, although Wall and Perry (1987) suggest dispersal distances for Lepidoptera pheromones in the range of 200–500 m, with larger attraction ranges for some species of moth. However, regardless of the effective attraction range of the pheromone, the plume is likely to disperse more readily and further when positioned on the woodland edge rather than within the interior of the woodland (Murlis *et al.*, 2000). Hence, the effective attraction range of OPM pheromone traps positioned within the canopy of oak trees inside the woodland block is likely to be a relatively short distance compared with those traps positioned at the edges of oak stands or on isolated trees.

In the present study, it appeared that aspect was not a significantly influential factor, although the prevailing wind direction is likely to have influenced the direction of the pheromone plume and hence contributed to the efficiency of the pheromone trap in attracting and capturing moths. Traps positioned on the leeward side of woodland blocks (north and eastern edges) were shielded from the prevailing wind for the majority of the month of August (Fig. 2), allowing the pheromone to disperse outwards, without being disrupted, away from the woodland block. Because male moths generally orientate upwind to pheromone plumes, male OPM would have flown into the wind and hence towards the pheromone traps on the north and eastern sides of woodland blocks, which is where they were more likely to be captured in the first traps they encountered (i.e. the traps on the leeward edge). Studies on other insect pests have similarly shown that wind direction can influence pheromone trap catches, with several studies reporting that more insects are captured on the leeward side, particularly when wind speeds are strong or moderate (Sappington & Spurgeon, 2000; Reardon *et al.*, 2006). Conversely, traps that were positioned on the windward side of woodland blocks (south and western edges) would have led to the pheromone being blown into the woodland block. Because OPM pheromone traps are positioned high up within the canopy layer, the foliage of the canopy is likely to have caused fragmentation and random dispersion of the pheromone plume as it was blown into the interior of the woodland block, making it difficult perhaps for male OPM to orientate to the traps on the windward edges. Previous studies investigating plume dispersion have found that tree composition and density within forests are factors that influence the extent of the fragmentation and dispersion of the pheromone plume (Thistle *et al.*, 2004; Peterson *et al.*, 2010); however, these and other similar studies have tended to investigate the dispersal of the plume under the tree canopy rather than through it.

The ability of a trap to capture a solitary moth over an entire trapping season is not particularly informative, especially because male OPM are reported to be able to disperse over distances of more than 50 km (Battisti *et al.*, 2015), although considerably shorter distances are far more realistic. Traps that only capture solitary moths, or at best a couple of moths, do not provide information on potential OPM nest numbers within a reasonable proximity to the trap, whereas traps that capture more than just a few moths would imply that there are OPM nests somewhere in the vicinity of the trap. This poses a key question of what number of moths in a trap is actually significant and informative, which forms the basis of subsequent investigations. However, as a starting point, we investigated the potential of traps to catch five or more moths and found that traps positioned on the edges of woodland blocks were significantly more likely to capture five or more moths than traps positioned within the

woodland block itself. This tended to confirm that it is essential to position pheromone traps in *Q. robur* trees in more open areas rather than within the interior of forests and woodlands when aiming to monitor the spread of OPM as effectively as possible as it spreads into more rural areas in the south of the U.K.

The results from the present study have demonstrated that the positioning of pheromone traps for OPM within the tree canopy is a highly influential factor. In addition to the trap needing to be positioned above 10 m to be effective (Breuer *et al.*, 2003; Williams *et al.*, 2013), traps also need to be ideally positioned more specifically in the canopy of *Q. robur* trees either on the edges of woodlands or in trees in more open habitats. Further studies investigating the role that VOCs might play in the attraction process of male moths to traps may assist in the further development of more effective lures for OPM, thereby increasing the efficiency of the pheromone trap further. In addition, future studies into the VOC composition of oaks may shed light on the orientation behaviour of the female moths to host trees, which in turn could be used to develop alternative management or control strategies for dealing with this invasive insect pest.

## Acknowledgements

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